POST-FIRE SEEDLING ESTABLISHMENT OF *ADENOSTOMA FASCICULATUM* AND *CEANOTHUS GREGGII* IN SOUTHERN CALIFORNIA CHAPARRAL

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ABSTRACT

Mortality of *Ceanothus greggii* and *Adenostoma fasciculatum* seedlings during the first growing season after a burn in the southern California chaparral was 92 and 90%, respectively. Survival of these shrub seedlings was not affected by the presence of stump sprouts, which grew at a rate of 2 cm in height per week, or by herbaceous plants (65% cover). However, the presence of annuals reduced the growth of the shrub seedlings significantly. Watering increased seedling growth, but additional fertilizer had no significant effect. Stump sprouting and abundant seedling establishment after fire appear to be main factors that insure maintenance of the shrub species composition of the frequently fire-disturbed chaparral vegetation.

Chaparral in southern California burns at 25- to 40-year intervals, although lower or higher fire frequencies occur (Philpot 1977, Keeley 1982). In spite of these repeated perturbations, the vegetation regenerates rapidly. This phenomenon of fast chaparral re-establishment after fire has been described in detail for a number of different California localities (e.g., Sampson 1944, Horton and Kraebel 1955, Hanes 1971, Keeley and Keeley 1982). From these observations, it can be concluded that the shrub species establishing during the first growing season after a fire are the same ones that composed the pre-fire chaparral community (Hanes 1971). However, the quantitative composition of the shrub cover may change. Assessment of the cover values for *Ceanothus crassifolius* and *Adenostoma fasciculatum* in a 15-year-old stand in the San Gabriel Mountains in 1934 and the re-assessment in 1982, 22 years after a burn, showed that the cover value for the former species had increased by the factor of two while the latter species had declined correspondingly (Jacks 1984).

Although these observations indicate the importance of stump sprout and seedling densities after fire for mature stand composition, little is known about the factors that influence shrub seedling establishment. The importance of the post-fire physical environment has been emphasized (Sauer 1977). Competing seedlings in the early establishment phase can modify the environment, for example through rapid water and nutrient uptake. It is unclear to what degree

MADROÑO, Vol. 32, No. 3, pp. 148–157, 19 August 1985

shrub seedling establishment is influenced by spatially variable factors such as the presence or absence of nearby stump sprouts. The competitive action of the sometimes dense but short-lived herbaceous vegetation on shrub seedling establishment is likewise unclear. Selective herbivory by rabbits on shrub seedlings has recently been documented (Mills 1983).

The objective of the present study was to obtain quantitative information on shrub seedling mortality and establishment. The data may improve our predictive capacity of mature chaparral stand composition.

Materials and Methods

Research site. The study site was the Sky Oaks Biological Field Station at 1500 m elevation about 15 km north of Warner Springs, San Diego County, California. The climate of the area is Mediterranean; and the site receives annually about 550 mm of precipitation between November and May. Some thundershowers interrupt the long summer drought. In most winters some snow remains on the ground for a few days. Minimum temperatures of −8°C and summer maxima of 38°C have been observed (Bowman 1984).

The research site was covered by a dense, 54-year-old shrub vegetation (aged by year ring counts, P. Zedler, pers. comm.). Pre-burn analysis showed a density of 1.01 shrubs per m^2; *Adenostoma fasciculatum* and *Ceanothus greggii* were the most important species, with 0.42 and 0.40 individuals per m^2, respectively. We observed the spotty occurrence of *Cercocarpus betuloides* Nutt., and *Quercus dumosa* Nutt. mostly on north-facing slopes and the tree *Quercus agrifolia* Neé. in ravines and washes. The soil is a loamy sand with abundant stones and pebbles. The soil layer, varying between 30 and 50 cm depth, rests on bedrock of a micaceous schist (USDA 1973).

In December 1981, a 2-ha site in this area was burned with the help of the California Department of Forestry and the U.S. Forest Service. The burn was complete and temperatures at the soil surface reached about 350°.

Shrub seedling establishment. Seedling establishment of *A. fasciculatum* and *C. greggii* was assessed post-fire on eight 8 × 2-m plots randomly distributed over the area. In each plot the shrub seedlings of ten 0.25-m^2 subquadrats were counted on 8 May and again on 11 December (i.e., 6 and 13 mo post-fire). Repeated counts from mid-April to the beginning of May indicated no further increases in the number of shrub seedlings; by mid-December the initiation of sustained rainfall made further drought-induced seedling mortality for the current year improbable.

Effect of stump sprouts and annuals on shrub seedling growth. To assess the effect of stump sprouts and annuals on growth of shrub seedlings, twelve 1-m^2 plots, each with a stump-sprouting *A. fasciculatum* in the center were distributed randomly over the 6 mo-old burn area in May 1982. Four replicate plots were established for each of the following treatments: (A) all stump sprouts removed, (B) all stump sprouts and annual herbs removed, and (C) control. Shrub seedlings were counted and their heights recorded biweekly. Stump sprouts and annuals in treatments (A) and (B) were removed with each observation date. The stump sprouts were carefully broken off by hand in order to avoid major wounding of the burls. New sprouts appeared during the entire year after the burn.

Irrigation and fertilizer application. On the burn site, twelve 1-m^2 plots without stump-sprouting shrubs and a minimum of five second-year *C. greggii* and *A. fasciculatum* seedlings each were fenced in the spring of 1983 with 0.5-m tall chicken wire to prevent small-mammal herbivory. Shoots that grew from adjacent stump sprouts into the plots were removed. Three treatments, consisting of four replicates each, were established. (1) Fertilized and watered: 10 liters of full-strength Hoagland's solution, containing 2 g N, 0.3 g P, and the other nutrients in corresponding amounts, were applied to the plots with sprinkler cans. The fertilizer application was repeated four times in two-week intervals between the beginning of June and the end of July. Water and fertilizer application was initiated in early June when soil moisture in the 10–20-cm depth layer had declined to about 3% (g H_2O g^{-1} dry weight; Fig. 1) and herbaceous plants showed symptoms of water stress. From January to June 1983, a total of 650 mm of precipitation fell. Thus, soil moisture remained relatively high until the end of May. Each fertilizer plot received 8 g N and 1.2 g P. (2) Watered only: Irrigation consisted of 10 liters m^{-2} of de-ionized water applied at the same times as the nutrient solution. In addition, the "fertilized and watered" and the "watered only" plots received a total of 80 liters of de-ionized water (20 liters per application) between the end of June and the beginning of September. (3) Unwatered plots.

In September and November 1983 the heights and crown diameters (maximum and minimum lengths between distal branch tips) of five representative seedlings per plot of *A. fasciculatum* and *C. greggii* were recorded. The crown diameter values were more meaningful than height values because branches elongated relatively more than the main leader shoots.

Biweekly gravimetric soil measurements in depth layers of 0–10, 10–20, and 20–30 cm, about one meter distant from the control plots of this experiment, provided basic information on the seasonal fluctuation of soil moisture in the rooting zone of the shrub seedlings.

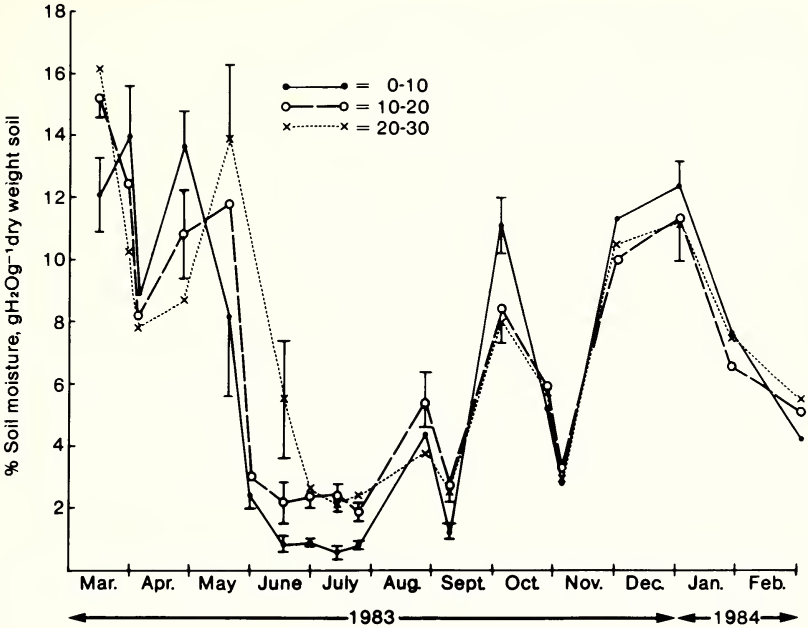

FIG. 1. Soil moisture one meter from the control plots of the irrigation and fertilizer experiment. Each data point is the mean of four samples. Vertical bars indicate standard errors.

Five representative seedlings each of both the species were excavated in bimonthly intervals. Although some root breakage appeared to be unavoidable especially in late summer, we think that the main roots were mostly recovered to their full extension.

RESULTS

Shrub seedling establishment. Abundant rainfall occurred during the first post-fire period (566 mm fell from July 1981–June 1982, Ellis et al. 1983). Thus the conditions for seed germination were favorable. In May 1982, an average of 78 shrub seedlings (34 *A. fasciculatum* and 44 *C. greggii*) per m^2 were counted (Table 1). In December 1982, 9.8% of the *A. fasciculatum* and 7.8% of the *C. greggii* seedlings were still alive. Periodic counts showed that most of the seedlings had died in May and June (Fig. 2).

Effect of stump sprouts and herbaceous plants on shrub seedling growth. Survival of *C. greggii* and *A. fasciculatum* seedlings during the first post-fire growing season was not affected by the presence of stump sprouts or herbaceous plants (the latter with ca. 65% cover). However, seedling growth was reduced by about ⅓ under the influ-

TABLE 1. MEAN NUMBER OF *A. fasciculatum* AND *C. greggii* SEEDLINGS AT BEGINNING AND END OF THE FIRST POST-FIRE GROWING SEASON. Values are means ± standard errors of eighty 0.25-m^2 plots randomly staked on eight 2 × 8-m observation areas.

A. fasciculatum			*C. greggii*		
Mean no. of seedlings m^{-2}		% surv.	Mean no. of seedlings m^{-2}		% surv.
May 8	Dec. 11		May 8	Dec. 11	
33.6 ± 12.96	3.3 ± 1.34	9.8	43.8 ± 7.84	3.4 ± 0.97	7.8

ence of the herbaceous vegetation (Table 2). Removal of stump sprouts did not enhance seedling growth, although these stump sprouts grew vigorously at an elongation rate of about 2 cm per week from May to October (Fig. 3). This indicated an adequate water supply for stump-sprouting *A. fasciculatum* shrubs during the summer of 1982.

Irrigation and fertilizer application. Biweekly gravimetric soil moisture measurements in the vicinity of the experimental plots demonstrated that by mid-June 1983, the soil in the upper layer had already dried out and only the 20- and 30-cm layer was still holding a small moisture reserve (Fig. 1). Our periodic seedling excavations

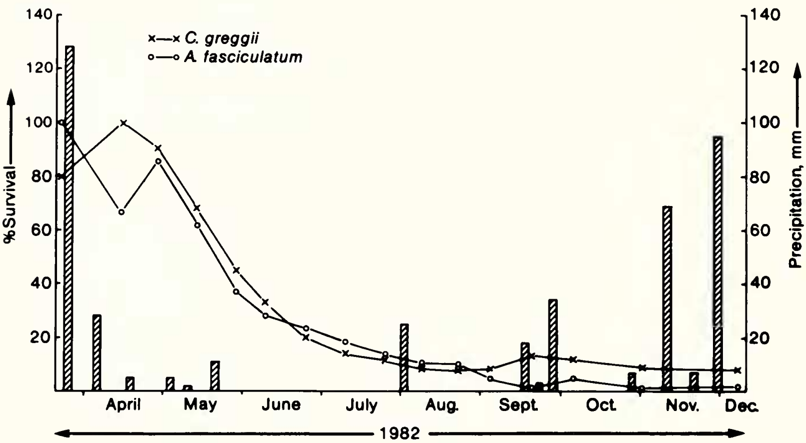

FIG. 2. Survival of *Ceanothus greggii* and *Adenostoma fasciculatum* seedlings which had germinated between February and March 1982, following a burn in December 1981. The highest observed seedling density was considered 100%. Each point is the mean number of seedlings in eight 1-m^2 plots. There was no significant difference in seedling survival between species. The hatched bars indicated rainfall events in mm.

TABLE 2. HEIGHT (mm ± S.E.) OF *C. greggii* AND *A. fasciculatum* SEEDLINGS AT THE INITIATION OF THE OBSERVATIONS (4/28/82) AND AFTER 10 WEEKS UNDER TREATMENTS A (STUMP SPROUTS REMOVED), B (STUMP SPROUTS AND HERBACEOUS PLANTS REMOVED), AND C (UNCHANGED CONTROL). Significance of differences among treatments indicated with different letters. Number of observed seedlings in parentheses. Statistical treatment: Basic statistics, ANOVA on log-transformed data, Newman-Keuls multiple comparison tests. [1]$p < 0.01$. [2]$p < 0.05$.

	C. greggii		*A. fasciculatum*	
	Initial height 4/28	Final height 7/9	Initial height 4/28	Final height 7/9
A. Stump spr. removed	10.5 ± 0.6a (32)	21.0 ± 1.3a (26)	9.8 ± 0.5a (31)	27.8 ± 2.0a (21)
B. Stump spr. + herbs removed	10.1 ± 0.6a (30)	35.5 ± 5.3b[1] (11)	10.4 ± 0.6a (40)	33.1 ± 3.7b[2] (24)
C. Control	10.4 ± 0.6a (30)	25.7 ± 3.7a (11)	7.6 ± 0.4b[2] (40)	21.9 ± 2.3a (14)

showed that at this time the main roots of these 2nd-year seedlings had reached a length of 20–30 cm. By the end of August and again at the beginning of October 1983, heavy thunderstorms produced enough rain to remoisten the soil profile down to 30 cm (Fig. 1).

On 9 September, the seedlings of both shrub species were larger in both the watered and the watered and fertilized plots. Six weeks later (21 October) this difference was still visible, although not statistically significant in the case of *A. fasciculatum* (Table 3).

DISCUSSION

More than 90% of the seedlings that germinated in March and April 1982 after a fire in December 1981 died during the first growing season. Our biweekly observations had shown that May and June were the months with the highest mortality. These values seem high when compared with others (Musick 1972, Keeley and Zedler 1978, Horton and Kraebel 1955), although exact shrub seedling mortality rates in the spring following a fall fire are poorly quantified (Schlesinger et al. 1982).

We can deduce from precipitation data that drought conditions became severe in May and more so in June (Fig. 1). Excavation of five seedlings each of *A. fasciculatum* and *C. greggii* in July 1982 showed mean tap root lengths of 5 cm and 8 cm, respectively (Ellis 1983). Thus, lack of soil moisture is probably one of the factors causing the high seedling mortality. A second cause for the death of many seedlings was herbivory. By November 1982, 25% of the *A. fasciculatum* and 43% of the *C. greggii* seedlings on this specific research site had been killed by rabbits (Mills 1983).

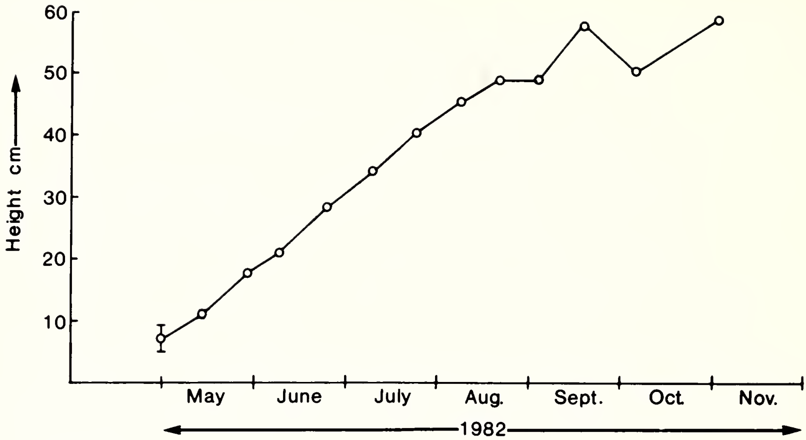

FIG. 3. Growth in height of *Adenostoma fasciculatum* stump sprouts during the 1982 growing season after a burn in December 1981. Ten average-sized shoots of 4 randomly chosen *A. fasciculatum* stumps were measured. A typical standard error is indicated for the first (May) value. Note the linear height increase during the dry summer months.

Very little is known about the effects of the herbaceous post-fire vegetation on shrub seedling establishment. We could not find evidence for increased survival of shrub seedlings when competing stump sprouts and herbaceous plants were eliminated, although roots of the stumps must have remained active. This result contrasts sharply with data shown by Schultz et al. (1955). A grass density of 85% eliminated all shrub seedlings, and a grass density of 18% reduced the number of surviving shrub seedlings by 50%. An explanation for these conflicting results may be that grasses were virtually absent from our research site, whereas the above-mentioned observations were made on a burned and ryegrass re-seeded area. Ryegrass plantings have been shown to inhibit herb establishment and chaparral seedling growth (Corbett and Green 1965). In our site the estimated herbaceous cover was about 65% and consisted mostly of the native fire followers, *Phacelia brachyloba, Streptanthus heterophyllus,* and *Gilia caruifolia,* all with much less aggressive tap root systems than the fibrous root system of ryegrass (Rice and Green 1964).

Although seedling survival was not affected by stump sprouts of *A. fasciculatum* and the herbaceous vegetation, we found that herbs caused a significant growth reduction of the shrub seedlings. The vigorously growing *A. fasciculatum* stump sprouts did not affect shrub seedling growth. These stump sprouts, consisting of clusters with about 150 shoots per burl, grew at a rate of about 2 cm per month from April to October, when they reached a final mean height

TABLE 3. RELATIVE SIZE (HEIGHT OF THE MAIN SHOOT × AVERAGE DIAMETER) OF *C. greggii* AND *A. fasciculatum* SECOND-YEAR SEEDLINGS WHICH WERE NOT WATERED, WATERED, AND WATERED + FERTILIZED, THREE AND FOUR MONTHS AFTER TREATMENT INITIATION. For each treatment n = 19. Statistical treatment: One-way ANOVA on log-transformed data followed by Newman-Keuls multiple range test. Significant differences among treatments for each observation date indicated with different letters ($p < 0.05$). Standard errors given in parentheses.

Observation date	*C. greggii*		*A. fasciculatum*	
	9/9/83	10/21/83	9/9/83	10/21/83
Unwatered	24.3 (3.7)a	30.0 (4.7)a	72.1 (22.0)a	91.1 (12.7)a
Watered	62.1 (11.7)b	71.4 (13.5)b	100.4 (18.8)ab	127.9 (26.1)a
Fertilized + watered	53.0 (9.2)b	61.6 (10.6)b	117.3 (9.6)b	133.4 (13.9)a

of ca. 50 cm (Fig. 3). The fine root density around the burls was several times higher than that around the stems of unburned control shrubs (Kummerow and Lantz 1983). The fine roots of resprouting burls were predominantly located at about 20–30 cm depth, and thus were deeper than the roots of the ½-yr shrub seedlings, which had hardly reached a depth of 10 cm (Ellis 1983). However, roots of annuals and shrub seedlings occupied the same depth zone of the soil and might have competed for the same resources. Continued observations are needed to establish if 2nd- and 3rd-year seedling mortality is higher among seedlings whose growth was retarded by competing annuals and stump sprouts.

The fertilizer and irrigation experiment tested if resources might limit shrub seedling growth in the second post-fire year. The shrub seedlings reacted with a significant growth increase to fertilizer and water addition. The differences between the irrigation only and irrigation + fertilizer treatment in *A. fasciculatum,* although suggestive, were not statistically significant (Table 3). Thus, no clear indication for nutrient deficiency was found.

Overall, the results of this study show that drought is a main factor for shrub seedling mortality in the first year after a burn. During the second year, the seedlings responded with enhanced growth to fertilizer and water addition. The results suggest that the sprouting burls of *A. fasciculatum* plus the abundant seedlings of this species and of *C. greggii* provide more than enough plants to insure perpetuation of these shrubs even after an initial mortality of more than 90% during the first post-fire growing season. Mortality during the second year was insignificant.

ACKNOWLEDGMENTS

This study was supported by NSF-Grant No. DEB-8025977-01. Dr. David Rayle helped in revising a first draft; assistance from Ms. Mildred Johnson and Ms. Robin McQuitty with the manuscript preparation is gratefully acknowledged.

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(Received 26 Oct 1984; accepted 15 Feb 1985.)

ANNOUNCEMENT

The first segment of a flora for Butte County, California, on the Boraginaceae, initiates the series "Publications from the Herbarium, California State University, Chico." This 35-page pamphlet contains keys to the 31 taxa occurring in Butte County, brief descriptions of the plants, their habitats and (from the literature), their reproductive biology. Thirty detailed range maps are included. For a copy please send $2 to ROB SCHLISING, Department of Biological Sciences, California State University, Chico, CA 95929.

ANNOUNCEMENT

A regional reference herbarium has recently been established at Deep Springs College (located at the south end of the White Mts. in Inyo Co., CA). As curator *in absentia* and a recent alumnus, I am seeking contributions of duplicate specimens from the White Mts., Deep Springs Valley, and the adjacent basins and ranges. A few more exotic species would also be welcomed for teaching purposes. Very common species are already well represented and should be avoided. The collections can be made accessible to outside workers through prior arrangements with the college, and a standard herbarium designation will be obtained when sufficient size is reached. Inquiries or unmounted specimens may be sent to: Professor of Biology, Attn: HERBARIUM, Deep Springs College, CA, *via* Dyer, NV 89010. Specimens received will be acknowledged as tax-deductible contributions; correspondence will, if necessary, be forwarded to me.—JAMES D. MOREFIELD, NAU Box 6201, Northern Arizona Univ., Flagstaff 86011.